Taxonomy of lower categories—suggested guidelines

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Introduction

In the 1940s came a wider realization that evolution provides the theme for all aspects of biology. One of the pillars of this synthesis was a "biological" species concept, sponsored then and later by Mayr (1942, 1963), among others. Reduced to essentials, a species is a self-contained, interbreeding, interfertile population. Each such reproductively isolated species is forever on its own—to evolve, to adapt, or to face extinction. Such species, and the individuals comprising them, constitute the diversity and richness of life on earth. Recently this species concept has come under scrutiny and some opposition. On the one hand the virtual explosion of new laboratory techniques, here subsumed under the rubric "molecular biology", has permitted penetrating analyses of populations. In another direction, more rigorous cladistic methods of phylogenetic analysis, associated in part with the work of Hennig (1966), pose new questions.

Several other species concepts have been proposed in recent years. Meanwhile the scientific community and the public at large continue to rely on the prevailing understanding of this taxon. The biochemist seeking a vaccination for malaria assumes that he has been correctly informed by the taxonomist that the mosquitoes before him are the vector of a particular strain of malaria. The conservationist assumes that the species he is seeking to preserve are realities.

We briefly review some conflicting species concepts and conclude that, while they shed new information on the complex and variable evolutionary process of speciation, they pose no threat to the belief, may one call it a fact, that the vast majority of living organisms are (or for fossils, *were*) organized into the self-contained interbreeding units, which Noah, loading his Ark, called species. Our main purpose is to present an ordered scheme of categories dealing with taxa at or near the species level. As we make clear below, one is obliged in consideration of taxa at any given level, to treat matters to the next higher level (here, the genus) and to the next lower level(s), subspecies and even demes. Others have initiated this process, piecemeal, as indeed have we (see References). A few new terms are defined as necessary to complete the framework.

The working taxonomist is faced with various problems. New terminology is rife; we attempt to separate what is useful from what is superfluous or impractical. Taking it for granted that since the time of Darwin classifications should embody as much as possible of known or presumed phylogeny, to what extent can the veritable flood of information and theory from molecular biology and cladistics be incorporated into a classification, and what part left to cladograms or other means of presentation? Must not a classification also reflect degree of change; after all to evolve is to change over time. If on some planet the only result of 3 or 4 billions of years of evolution were 200 or 300 nearly identical species of "seaweeds", how significant would a cladistic analysis of their phylogenies be? Linnaeus, a century before Darwin, set up his higher categories because he realized that, for example, seals are less closely related to cats than is one genus of cat to another. Several of the definitions refer to monophyly. Some groups have so many traits in common, that monophyly can scarcely be questioned; e.g. the living species of flamingoes (Phoenicopteridae). Often however, especially when based on fossil specimens, few and imperfect, monophyly is a tentative conclusion. The methods and special taxonomy of cladistics are of assistance, though fossils pose major problems (Van Valen 1978). Molecular biology plays an increasing role but with rare exceptions is limited to living or recently extinct organisms.

Definitions of terms

To facilitate discussion we begin by defining the terms that we find essential or useful. The numbers correspond to those in the following analysis. Three terms, marked with an asterisk, are here introduced for the first time. Four of the terms: species, subspecies, genus, subgenus are formal designations, rules for whose usage are set forth in the Rules of the International Commissions on Nomenclature—botanical and zoological.

1—SYMPATRIC (SYMPATRY). Taxa that occur in the same area (range) at least in part and at least during the reproductive season.

2—ALLOPATRIC (ALLOPATRY). Taxa whose ranges do not overlap, at least during the reproductive season.

a—PARAPATRIC ALLOPATRY. Allopatric taxa whose ranges are (in part) contiguous, but do not overlap.

b—DISJUNCT ALLOPATRY. Allopatric taxa whose ranges are spatially separated.

3—DEME. Within a species, a localized diagnosable subpopulation of less than subspecies rank.

4—SUBSPECIES. Within a species, a named, recognized allopatric subpopulation which is (still) genetically compatible with other subpopulations, but is set apart by a concordant array of genetic and phenotypic characters.

5—MESOSUBSPECIES*. A subspecies that is not approaching species status.

6—MEGASUBSPECIES. A subspecies that is approaching species status.

7—SUBSPECIES GROUP. A monophyletic subset of subspecies within a species.

8—(SEXUAL OR GAMETIC) SPECIES. A freely interbreeding, interfertile, self-contained population (or group of subpopulations) of organisms.

9—MONOTYPIC SPECIES. A species without recognized subspecies.

10—POLYTYPIC SPECIES. A species with recognized subspecies.

11—MESOSPECIES*. A polytypic species none of whose subspecies is approaching species status.

12—MEGASPECIES. A polytypic species composed of megasubspecies. (Term introduced by Crawford-Cabral 1986.)

13—ISOSPECIES*. A species that is not a member of a contemporary superspecies, i.e., that is not an allospecies.

14—ALLOSPECIES. One of the allopatric species comprising a superspecies.

15—SIBLING SPECIES. Species so similar phenotypically that they are hard to distinguish.

16—GENUS. A named, recognized, monophyletic group of species, in rank between the species and the family (or subfamily).

17—SUBGENUS. A named, recognized, monophyletic subset of species within a genus.

18—POLYTYPIC GENUS. A genus containing more than one species.

19—MONOTYPIC GENUS. A genus containing only one species.

20—QUASI-MONOTYPIC GENUS. A genus consisting of one superspecies.

21—SPECIES GROUP. A monophyletic subset of species within a genus or a subgenus, but not formally named (as are the genus and subgenus).

22—SUPERSPECIES. A group of allopatric species (hence allospecies) deemed to have been derived from (mega)subspecies of a single antecedent species.

23—BIOGEOGRAPHICAL UNIT (formerly, BIOGEOGRAPHICAL SPECIES). A term applied to ISOSPECIES and to SUPERSPECIES considered as equivalents; that is, the allospecies of a superspecies are not listed or evaluated separately.

24—ASEXUAL POPULATION, CLONE, or "SPECIES". A population in which no interchange of genes occurs among individuals.

Discussion of terms

1, 2—SYMPATRY, ALLOPATRY

From the definitions it will be evident that we consider parapatric allopatry and disjunct allopatry as two kinds of allopatry. Thus we do not follow Prigogine (1984, 1985) who recommended parapatry as a third category equivalent to sympatry and allopatry, limiting the latter to disjunct allopatry. Some subspecies of a species may be parapatric, as on a continent, with others disjunctly distributed on surrounding islands. The same is true of the allospecies of a superspecies. Furthermore, as a result of changes in sea level, orogeny, or climate, taxa which were once parapatric may become disjunct or vice versa. Such changes may at times occur abruptly, due for example to stream capture, volcanic eruptions, or the like. The degree of geographic separation may vary from slight (patchy distribution) to great (on different continents). It seems best to subsume parapatric allopatry and disjunct allopatry under allopatry.

Parapatry infers visual and vocal contact, and thus the opportunity for physical contact between individuals of 2 taxa in the appropriate season or time of year for breeding activity (subspecies and allospecies of birds may come into sympatry seasonally, through migration, when they do not breed). Taxa are not parapatric when, for example, they involve forest animals separated by a broad river which they do not cross, and across which they cannot hear or see individuals (but at the headwaters of such a river they may become parapatric).

The important fact is whether 2 taxa overlap and hence are *ipso facto* (sympatric) species or whether they are spatially separated and thus could be either subspecies or species. Taxa that are in parapatric allopatry are more profitably studied by the evolutionist than spatially separated ones because actual contact provides a test for the completion of speciation. Nevertheless, disjunct populations are a far more fertile source of new species, because of their often greater genetic isolation, and their frequent occurrence in more distinct ecotypes.

Smith (1965) proposed the term "dichopatric" for what we have called disjunct allopatry; the term disjunct had been used for this purpose at times. Mayr (1982a,b) proposed a term "peripatric" for instances of disjunct allopatry resulting from dispersal, hence "peripatric speciation." This will usually involve a small number of individuals, and will result in the "founder effect" of Mayr (1948a; see also Carson 1989). Cracraft (1984) agreed with this and went on to suggest that Smith's term dichopatric be restricted to the other class of disjunct populations, those resulting from vicariant events such as orogeny. He noted that in some biogeographic and other analyses, it is useful to make this distinction.

Still, the terminology leaves something to be desired because dichopatric was originally proposed to apply to *all* types of disjunct allopatry, while peripatric is doubly confusing both because of its similarity to parapatric (when spoken as well as in print) and because such peripatric populations are not parapatric but disjunct. That is, it is not a kind of parapatry. Probably in those instances where it is necessary to make the distinction, it may best be simply explained which type of disjunct allopatry is meant.

3—DEME

Species, except those with very small ranges, or perhaps wide-ranging promiscuous ones (some cetaceans), tend to become subdivided into allopatric, local, often weakly characterised, subpopulations called demes. Local populations of birds that have developed song dialects are examples. Such trends may at first have little or no genetic basis, but if dispersal and gene flow are minimal and isolation continues, these demes can evolve through subspecies to species. Or, adaptive gene combinations may become established more easily in small populations like demes and can then gradually permeate the entire species.

4—SUBSPECIES

When subspecies are in parapatric allopatry they interbreed and exchange genes where their ranges meet. This will usually not lead to genetic swamping and the merger of the subspecies, for each is often adapted to a slightly different ecotype. Equally important, however, as with demes, favourable gene combinations may spread throughout the species. The amount and nature of the gene flow are affected by population structure, dispersal rates, the distribution of preferred habitats, and other factors. The access of diverse populations to beneficial genes and gene combinations is potentially of great value, and is possible because of reproductive compatability. When variation is clinal, as is often the case, it is unwise to name subspecies unless the terminal populations are strikingly unlike. The same is true of non-concordant clinal variation; e.g., size may increase northwards and paleness westwards. Such variation may, to a degree, result from non-genetic (in the immediate sense) responses to slowly changing ecotypes. Put otherwise, most populations that warrant subspecific status will represent a more or less integrated suite of characters, some adaptive, some neutral.

The use of the term "recognised" in the sense of "visibly different" in our definition of the subspecies is deliberate. The formal naming of spatial subpopulations should be restricted to those that are morphologically (phenotypically, and proven or presumed genetically) separable at some reasonable level, e.g. 90%. This is as true now as it was a half-century ago when Bullough (1942) unwisely named the resident European Starlings *Sturnus vulgaris* of Great Britain a subspecies, *britannicus*, to separate them from the phenotypically inseparable, migrant Scandinavian Starlings, which overwinter in the British Isles.

Clamour for the abolition of the subspecies as a formal category has come mostly from those unconcerned with the broad aspects of geographic variation and speciation; for defence of the subspecies see, e.g. Smith & White (1956), Amadon & Short (1976). The usefulness of traditional and formally recognized subspecies was discussed in a series of short papers by Mayr (1982d) and others. Palaeontologists might be expected to have little need for subspecies, but Simpson (1961: 176) recommended "successional" (temporal) subspecies when analyzing some fossil sequences.

Many taxa known by intergradation or reasoned by inference to be conspecific are nonetheless so distinct that taxonomists, general biologists, conservation and government agencies, and laymen seek a name for them. By providing a subspecies name this need is met; further, the unfortunate tendency to elevate such infraspecific taxa to the status of species is lessened. In better known groups most such taxa already have names available.

The simple scanning of check-lists or other publications in which subspecies are listed can provide information and suggest lines of investigation for many studies of biogeography, biodiversity, ecology and evolution, including: comparison of genetic variability with phenotypic variability; analysing why some congeneric species show more variability than others; comparison of levels of differentiation associated with degree of geographic isolation; size of range (islands); and amount of variation in migratory versus non-migratory populations. Subspecies are increasingly recognized as important in environmental conservation and the maintenance of biological diversity. Government agencies can (and should) deal with named, definable subspecies, which provide a convenient, logical and biologically significant level of categorization for maintaining biodiversity (O'Brien & Mayr 1991). Endangered status, usually given when a species is reduced to a level below 5000 individuals, ought, for purposes of preserving significant genetic diversity, to be applied also at the subspecies level. Certainly this would serve the long-term goal of preserving biodiversity, and indeed species. It also obviates the need felt and too often expressed by some conservationists, to inflate subspecies to the level of species solely to preserve them.

To be sure, too much emphasis upon subspecies when shaping public policy can occasionally be a double-edged sword. Efforts to save the gravely endangered Florida population of the cougar or "panther", *Felis concolor*, have been questioned because apparently a few individuals from Central America, which *may* represent a slightly different subspecies were at one time released in Florida, thus "tainting" the local population. But surely the important point is to save the only remaining remnant of the species in the eastern United States.

Subspecies are accepted by Avise & Ball (1990); to qualify as a subspecies they ask that a population exhibit concordant characters, preferably demonstrated molecularly, but add that sometimes a concordance of phenotypic characters will have to suffice because it is too much to expect that all populations of organisms will be analysed genetically.

For those who would argue against formal recognition of the subspecies, it may be noted that this in no way alters the conclusion that there is a fundamental difference between infraspecies populations (not genetically isolated) and species (genetically isolated). Indeed, even those who may avoid formally named subspecies, will have to use some method of categorizing and ranking geographically isolated, distinctive, but infraspecific populations.

5—MESOSUBSPECIES*

A term here proposed for the great majority of subspecies, those that are not approaching species status. Mesosubspecies may be well-defined by one or more traits, some at a level of 100% separation from one another. Several mesosubspecies may form one megasubspecies of a megaspecies, presenting problems addressed by Amadon & Short (1976). A polytypic species comprised only of mesosubspecies (that is, lacking megasubspecies), is a mesospecies as defined above. Mesosubspecies may be clustered into subspecies groups, if that is desirable.

6—MEGASUBSPECIES

In an earlier paper we (Amadon & Short 1976) introduced this term and suggested procedures for the use of parentheses to indicate them. Thus *Circus* (*cyaneus*) *hudsonius* indicates that the North American form of the Northern Harrier is judged to be a subspecies of the Eurasian *Circus cyaneus*, but one which is approaching species status. The 2 are completely isolated geographically. In more general works merely the species name, *Circus cyaneus*, would be used for both.

There are a great many such taxa, hundreds in the Class Aves alone, whose status, whether species or megasubspecies, is in part a judgmental opinion. In the harrier example, the 2 megasubspecies are not greatly different, but the genus is one with some quite similar sympatric species, which suggests caution. On the other hand a third taxon, related to the 2 just noted, *cinereus* of South America, is much more distinct and we think it is a valid species. Then *cyaneus* and *cinereus* are the two allospecies of a superspecies *Circus* [*cyaneus*]. Thus the megasubspecies provides a repository for, as the definition states, taxa that, on the available evidence, are concluded not to have crossed the species threshold, but to be approaching it. (See also number 12, megaspecies, below.)

7—SUBSPECIES GROUP

The subspecies of polytypic species often permit separation into groups with shared characteristics, frequently along geographical lines. The category is informal, so one may use it without assigning all the subspecies in a species to subspecies groups (though it is often heuristic to do so), while recognizing that a single subspecies may form its own group. In megaspecies the megasubspecies themselves essentially constitute subspecies groups and it will rarely be worthwhile to attempt further groupings.

Because of "leapfrog" or mosaic evolution, disjunct subspecies occasionally are phenotypically more similar than parapatric ones. Or, for example, dark-coloured subspecies of larks or mice may occur wherever there is a sizeable outcropping of black lava. To associate such subspecies may result in groups that are not monophyletic, requiring careful taxonomic analyses.

8—SPECIES

Characteristics. A species is an interbreeding, interfertile (i.e. Mendelian) population of organisms. We have added "self-contained" rather than "kept separate from other populations (species) by isolating mechanisms". Carson (1989) favours such a concise definition as emphasizing the *sine qua non* of the species, a common gene pool, and notes that Dobzhansky (1950), the pioneer in applying genetics to the species concept, did the same.

The species is often, even usually, defined as "a group of interbreeding populations". This is misleading. Many, perhaps most, species evolve from a small isolated population—the "founder effect" of Mayr (1982a) or the "punctuated equilibria" (in part) of Gould & Eldredge (1977) (see also Barton 1989). Some species, because they always have small ranges, remain essentially panmictic; others become so as they decline towards extinction.

Most species do eventually break up into more or less spatially segregated subpopulations. But these subpopulations, from one point of view, disrupt the species away from panmixia; when sufficiently isolated and for sufficiently long periods, they will diverge through the stages of deme, mesosubspecies, megasubspecies, species, and even genus. To define the species as based upon or requiring interbreeding *populations* is quite simply an error, but subpopulations must be mentioned to make it clear that these usually arise and remain part of a species for indefinite periods.

Species vary over space and time and this, together with their intrinsic variability, as enhanced by sexual reproduction, open the way for the evolution of new species. It is not surprising that the species definition sometimes has to be qualified to cover specific cases, of which the 3 following are among the more significant.

(a)—As already noted, species, especially widely distributed ones, tend to break up into subpopulations. These may be in either parapatric or disjunct allopatry; some of the latter may be only "potentially" capable of interbreeding with other subpopulations, e.g. rats, *Rattus*, stranded on an island. Others, of course, are permanently stranded, as by the submergence of the Siberian-Alaskan Landbridge, yet such populations may remain conspecific for long periods.

(b)—Closely allied species (allospecies), sometimes continue to interbreed (hybridize) to a limited extent; an extent insufficient to undermine their genetic integrity (see later discussion).

(c)—Over geological time, fossil lineages must be arbitrarily broken up by the taxonomist into species, genera and families, keeping them as equivalent as possible to ones based on contemporary taxa. As Simpson noted (1961: 165), any species, living or fossil, e.g. *Homo sapiens*, could in theory be traced back generation by generation to a one-celled ancestor; but to designate such an entire lineage as a single species is "not only useless but somehow wrong in principle. Certainly the lineage must be chopped into segments (species, genera, families) for the purpose of classification and this must be done arbitrarily". Gaps in the fossil record, doubts as to exact lineage, and other factors make the process of subdividing such lineages less difficult than might be expected.

Bock (1986: 38) disagrees and concludes that species have no beginning and no end (except extinction). But if a species occurs in a Palaeocene fossil bed, for example, and a taxon in the same lineage in another deposit from the Eocene 15 million years later, but by now much changed, is there any recourse but to name it as new? To continue to use the name applied to a quite different earlier stage would be completely confusing.

Some cladists have tried to circumvent the problem of lineages over secular times by positing that every time a species buds off a new one, the parent species, too, becomes a "new" species. Nonetheless, assume that seeds of an African tree, for example, were blown to St. Helena Island, where they were picked up and planted by Napoleon in 1817 or 1818. If and when they diverge to the species level are we to suppose that the African tree, which continues on virtually unchanged, is to be designated a new species also? At what point in time is this to be done? Some trees in China and the Appalachians are so similar after many millions of years of separation that they may still represent only subspecies.

Related species are kept from interbreeding by so-called (reproductive) isolating mechanisms. These are of 2 chief kinds: pre-zygotic (pre-mating) and post-zygotic (post-mating). Pre-zygotic barriers include vocalizations, odours (pheromones), 'courtship' displays (birds, fruit flies), and even patterns of light flashes (fireflies, Lampyridae). Such mechanisms seem insubstantial and indeed may begin as non-genetic variations, e.g. song dialects among birds. If isolation continues and is sufficient, they will acquire genetic bases; in the same period of time other distinctions will arise and, if secondary contact between 2 such groups occurs, may act as supplementary isolating mechanisms.

Post-zygotic isolating mechanisms run the gamut from complete sterility, through sterile hybrids (e.g. mules), to more or less fertile hybrids which, however, may possess subtle disadvantages in nature. In all such cases natural selection will tend to reduce costly mis-matings, which leave no long-term, viable offspring and which may even result in hardy 'mules' that compete with both parent species. An exceptional case is provided by certain flightless, very sedentary, Morabine grasshoppers in Australia, populations of which are prone to acquire chromosomal alterations. When such populations meet parapatrically, they interbreed freely; there has not been time for pre-mating barriers to evolve (White 1978, Key 1968). If 2 such subpopulations prove intersterile, speciation has occurred (called 'stasipatric' speciation); if some genetic interchange is possible, they are megasubspecies.

The opposite occurs more commonly. Isolated populations gradually acquire differences that will later serve as pre-zygotic isolating mechanisms (in voice, odour, behaviour, etc.) before genetic changes are sufficient to ensure sterility (post-zygotic separation). When such populations come into secondary contact, cross-breeding will be rare; but when it does occur, more or less fertile hybrids may result.

A few instances are known in which normally reproductively isolated taxa, though not intersterile, for example on isolated mountains or on islands, have produced hybrid swarms (Short 1969: 96–97). This suggests that the hybrids may be superior under the insular conditions, that pre-zygotic isolating mechanisms are incompletely developed (or break down), and that post-zygotic isolating mechanisms are lacking.

Two Mexican finches, *Pipilo erythrophthalmus* and *ocai*, interbreed in most areas where they meet, but are sympatric without interbreeding in one area (Sibley 1954, Sibley & Sibley 1969). In a few other cases supposed species (allospecies) are being hybridized out of existence: hybrids and one of the parental species apparently are being selected for at the expense of the second species, e.g. the new Zealand Black Stilt *Himantopus novaezealandiae*, is being displaced by the Common Stilt *H. himantopus leucocephalus* (Pierce 1984) and the Black-eared Miner *Manorina melanotis* by the Yellow-throated Miner *M. flavigula* in Australia (R. Schodde and L. L. Short *pers. obs.*). In both cases there has been extensive modification of the environment by humans. It can logically be argued that in such cases the taxa are megasubspecies and not allospecies, because otherwise the presence of effective isolating mechanisms should make massive hybridization impossible between species. Extinction by hybridization should not occur in allospecies; if extinction does occur after secondary contract, it is because one of the allospecies proves to be selectively superior to the other and replaces (total extinction) or displaces (partial extinction) it through competitive exclusion.

There may be rare exceptions, e.g. an allospecies restricted to an island subject to extensive human modification, followed by secondary entry by an allospecies, could result in hybridization and breakdown. It is even possible that a hybrid swarm could be the end product of the evolution of 2 allospecies if all populations of those allospecies became extinct other than the hybrid swarm itself. It is significant that polyploid species of plants, or more rarely parthenogenic species of animals (lizards), survive, when they do, in ecotypes which have been much disturbed (usually by man).

Competing Species Concepts. As noted, a continuing flurry of publications on the species question has promulgated several different species concepts or definitions (Andersson 1990). While our approach is practical rather than theoretical, the species is so central to taxonomy and classification that it is desirable to discuss briefly some of these proposals as they relate to our proposed terminology. Aside from other publications cited herein, one may *inter alia* mention important ones by Chandler & Gromko (1989), Coyne *et al.* (1988) and Häuser (1987).

(a) *Evolutionary species.* Simpson (1961: 153), primarily a palaeontologist, proposed the following definition: "An evolutionary species is a lineage (an ancestor-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." The word lineage implies an interbreeding population, viewed over time. Thus the definition again comes down to *genetically* isolated populations. Indeed, Simpson stated that in an earlier published version of this definition he had included the word "interbreeding" but dropped it to include clones and asexual "species" (but see below).

With the inclusion of the element of interbreeding, the evolutionary species definition becomes equivalent to the biological one. It does emphasize the temporal element: that species (and life) are a succession of individuals and populations. Indeed, only these 2 definitions are readily applicable to fossil as well as extant taxa. It further emphasizes that species have roles and tendencies, and as noted below that they have individual ecological niches. This need not be appended to the definition.

(b) *'Ecological' species concept.* Mayr (1982c: 273) and others (Hengeveld 1988) have added to the species definition that each species will have its own unique ecological niche. Simpson's "evolutionary" definition has ecological implications, while Van Valen (1976) also casts a species definition in ecological terms. Sympatric species, no matter how similar (sibling species) may be assumed to have ecological (niche) distinctions (Gause's principle). Yet there would seem to be no theoretical reason why allopatric species need differ ecologically. An insectivorous mole, *Talpa*, on one island and a marsupial mole, *Notoryctes*, on another, might in theory occupy identical ecological niches, yet they would be not merely different species but belong to separate sub-classes of Mammalia. No stipulation about ecology is needed in the species definition.

Somewhat similar is the occasional statement that speciation has not been "completed" until the 2 allied taxa have acquired overlapping (sympatric) ranges, which derives from the simple and pragmatically useful fact that sympatry provides the ultimate test for the efficacy of reproductive isolating mechanisms. If speciation is not complete when 2 allospecies happen to come into secondary contact, it may undergo refinement and reinforcement during parapatry and limited sympatry (e.g. the *Passerina* bunting case discussed below). Some parapatric species remain too similar ecologically to overlap; each of course is apt to be better adapted to a distinct microecotype within the main part of its range. In a few cases a new species may deviate so far ecologically from its immediate ancestors or nearest allies that overlap is out of the question, e.g. the first cetacean to become independent of land.

(c) *'Recognition' species concept*. Paterson (1985) concluded that the important element in species formation is not how individuals of a species avoid mating with those of other species but how they recognize individuals of their own. The former he calls the "isolation concept" and thinks it needs replacing. Others (e.g. Mayr 1986) regard these as 2 sides of the same coin: e.g. a male moth is attracted by pheromones emitted by females of his own species and ignores those of others. In plants and many lower animals recognition consists of reacting to another individual with the "right chemistry." "Recognition" may be by only one sex; male Pin-tailed Whydahs *Vidua macroura* and Straw-tailed Whydahs *V. fischeri* court any small brown bird that approaches, even unrelated serins *Serinus* spp.; further the 2 whydahs maintain interspecific territories, but their females only breed with the "correct" males (Short & Horne, *pers. obs.*). In sympatry, species are self-defining and thus are the only self-defining evolutionary unit. Taxonomists search for areas of sympatry between closely related taxa as the ultimate test of their status as species, allospecies or megasubspecies, and in order to gain insight into the nature of differences that obtain between related but allopatric taxa, the better to evaluate their status.

Isolating mechanisms vary, and under stress (lack of appropriate conspecifics, as in captivity), interbreeding often occurs between species never, or very rarely, known to hybridize in the wild. Also there are situations involving dynamic interactions of allospecies as they initially come into secondary contact, in which hybrids occur commonly at first, and then, as sympatry increases, hybridization ceases. An example is the movement of the Syrian Woodpecker *Picoides syriacus* into the central European range of its allospecies, the Great Spotted Woodpecker *Picoides major* (Bauer 1957). Such biological "mistakes" (due to lack of post-zygotic isolating mechanisms and breakdown of pre-zygotic isolating mechanisms), which may occur when the expanding species is rare and its potential conspecific mates are few, should not be interpreted to mean that the 2 taxa involved are conspecific. Sometimes, of course, a time span is required to be certain. In these cases strict application of Paterson's concept would mean that, when initially interbreeding, these taxa would be conspecific, but when hybridization ceased they would "become" species. Paterson's work will, however, bring more attention to the evolution of the crucial isolating stimuli involved in speciation. It should also prompt research on other forms of species recognition.

The species recognition associated with reproductive isolation of species is not unique to that facet of biology, nor is it always successful. African estrildine finches have characteristic, species-specific gape markings as nestlings, but nestlings of nest-parasitic widowbirds (*Vidua* spp.) mimic the gape markings of these estrildine nestlings, species for species, thus making it possible for the widowbirds to use the estrildines as foster parents for their own young (Payne 1982).

Interspecific territoriality is akin to recognizing other species as if they were conspecific and is thus a failure to show "species recognition", or rather is a broadening of the "recognition" to include other species. Many sophisticated adaptations have evolved for recognition of prey or host organisms (as by parasitic wasps, and nest-parasitic cuckoos), and of food plants by insect larvae and their adult forms, to give only a few examples. Within species there may be failure of "species recognition", as by birds of different local song dialects, that deter interbreeding of conspecific individuals of different demes (Payne 1986). Females of many species regularly reject as mates males in subadult plumage attempting to breed.

The biological species definition includes all aspects of the recognition of conspecific mates. It is thus inappropriate to designate the biological species concept as the "isolation" concept, either as a substitution for it or to compare it with the species recognition concept. For further discussion of Paterson's species recognition concept see Bock (1986: 41), Coyne *et al.* (1988), Häuser (1987), and Raubenheimer & Crowe (1987).

(d) *"Cohesion species concept"*. Templeton (1989: 12) wrote: "The cohesion concept species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms." He then tabulates these mechanisms. We need not reproduce his table, because the final product is close to our understanding of the species. All species have cohesion and Templeton rightly emphasizes this. To some extent it partakes of the "homeostasis" mentioned at various points by Mayr (1963). One may note that no species, if subdivided spatially, is so *cohesive* as to prevent differentiation and eventual formation of a new species. Asexual "species" on the other hand are too "cohesive"; adaptive change can take place only by the replacement of entire populations, one mutation at a time.

Templeton designated his cohesion species concept to accommodate both sexual and asexual populations. As discussed elsewhere, we do not consider this feasible.

(e) "Phylogenetic" species concept. This was introduced by Rosen (1973, 1979) and followed by others including Nelson & Platnick (1981) and Cracraft (1983). The phylogenetic species was recently defined by Cracraft (1989: 34–35) as "An irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." McKitrick & Zink (1988) recommended the phylogenetic species to ornithologists but gave nary an example of how they would apply it to any species as presently understood.

All more or less isolated subpopulations of a species acquire genetic differences, whether adaptive or by genetic drift. Founder populations would immediately qualify as "phylogenetic species"; their gene pool will differ from the larger one from which it has been drawn. Indeed DNA "fingerprinting", from one point of view, has reduced effective population size to a single individual. When such populations interbreed with neighbouring populations, or are capable of doing so, are they species? If so, one could easily find subpopulations of *Homo sapiens* that still, despite all the mixing that has gone on, qualify as "phylogenetic" species. Morphs of a single population may differ more than will many such phylogenetic species. In the White-throated Sparrow *Zonotrichia albicollis* for example, 2 morphs differ in colour, in osteology, and chromosomally, as well as in habitat preferences and song frequency (Thorneycroft 1966, 1975). Yet they are only morphs; individuals of one morph prefer to mate with the other. Mayr (1963: 247) listed a number of genera, including the lowly *Asellus*, in which morphs differ in habitat preference (and doubtless in other ways as well).

Avise & Ball (1990) also emphasize that the number of subpopulations diagnosable by molecular biology or even phenotypically is enormous. Further, if analyzed by differing techniques or for varying goals, the boundaries of these subpopulations will often not coincide. The many well established breeds and varieties of domestic animals (dogs, pigeons, etc.) or cultivars and varieties of plants (roses, tomatoes, etc.) are phylogenetic "species". They are kept separate by the hand of man; their counterparts in nature by spatial isolation.

Presented with the males and females of a highly dimorphic species (e.g. the sapsucker *Sphyrapicus thyroideus*) in which the sexes are easily diagnosed phenotypically—by the sex chromosomes and presumably (if they could be demonstrated) by certain genes controlling the dimorphism—how would one determine that they belong to the same species? *Because they interbreed.* Much molecular biology is based upon tissues of a few individuals. How does one know that the other individuals assigned to a species based on such samples belong to it? Again, because they *interbreed*, or are assumed to do so because of the phenotypic uniformity bestowed by interbreeding. Thus, we are again back to the interbreeding test for the species.

J. Fitzpatrick, quoted by McKitrick & Zink, estimated that the Florida Scrub Jay *Aphelocoma c. coerulescens*, itself an outlier of a western species, might have to be divided into 2 or 3 hundred species. This may have been tongue in cheek but is hardly an exaggeration. This multiplication of species would conceal, not reveal relationships. For example, if the geographically variable Song Sparrow *Melospiza melodia* were split into 30 'species', the related, less variable, *bona fide* species, the Lincoln's

Sparrow *Melospiza lincolni*, and the Swamp Sparrow *M. georgiana*, would tend to be lost in the shuffle.

Many such species would be undiagnosable in traditional museum practice; all old specimens would have to be identified subjectively and assigned to their species on geographic bases. Some of these might represent "temporal" species, because of biochemical evolution in the past 50 to 150 years after the type series and other museum material was collected. Fossil material would have to be ignored, or included subjectively.

We thus conclude that the proposal to call every diagnosable population a *species* is wrong in both fact and theory and would lead to chaos in application. That we are not overstating this point will be appreciated by those concerned with conservation decisions of governmental agencies, and the economics of conservation to the lay public, if they had to defend the preservation of every phylogenetic "species".

None of the above is meant to impugn the value of genetic and biochemical research in casting light on fundamental problems. If such research reveals an out-and-out error, as Zink (1988) has done in the *Pipilo crissalis/P. fuscus* group of finches, and this is supported by other data, by all means alter the classification to correspond with the newly discovered facts.

Practical considerations. How can a species be defined in terms of breeding behaviour when for all fossil species and many living ones, e.g. deep-sea fishes, we know nothing of breeding behaviour? The short answer is that biology is the science of life; species are populations of living organisms and there is no escape from this dilemma. Fortunately interbreeding and heredity do impart a certain uniformity to species. With most groups, given a mixed bag of specimens, one can sort them out into species with few errors. One may, to be sure, be misled by differences due to sex, age, castes, morphs or life stages, but this would be true whatever species concept was used. Once such problems have been surmounted, the identification of sympatric species usually offers no special problems. Some sibling species, especially among invertebrates, may, to be sure, remain unmasked until studied in the field or found in the laboratory to be inter-sterile.

Sympatric populations that do not interbreed, or not to an extent that undermines their genetic integrity, are perforce species. Closely allied species which have only recently or partially achieved sympatry may interact in various ways (limited hybridization, interspecific territoriality, or displacement of one by the other in some areas and not in others).

Parapatric populations present greater difficulties, but if they don't interbreed they are species, usually allospecies; if they do, they are subspecies. When limited or sporadic interbreeding occurs, the analysis must be more in depth; Short (1969, 1972) has presented procedures and guidelines for analyzing such cases. In general, if selection is reducing hybridization parapatrics are species, but not so if the reverse occurs. Often a long-term study is needed to find out, especially where parapatry is very limited. Most such instances are of secondary contact after evolution in isolation; it is doubtful whether primarily parapatric subspecies can advance to species status, except perhaps where there is an increasingly sharp break in their ecotypes. Many parapatric species meet along ecological gradients, but even if the change is very gradual, the 2 may abut sharply (e.g. see Short 1971 for 2 woodpeckers, *Picoides nuttallii* and *P. scalaris*, in the American Southwest). Rarely, as in the crows *Corvus corone* and '*C. cornix*' of Europe (Kryukov & Blinov 1989), a narrow but spatially shifting hybrid zone persists; this should not be taken to infer that they are allospecies. In this case the narrowness of the zone and its shifts reflect forces of selection and environmental gradients that are commonly found intraspecifically, and usually are inconspicuous, but in this example are conspicuous (the 2 crows are all-black vs black and grey). For example, there is a marked shift in tail-spotting of eastern and western populations of the American Robin *Turdus migratorius* over a few-score kilometers in the Great Plains, whereas the crows are megasubspecies, freely interbreeding throughout and are thus separated and yet connected by the hybrid zone. In an altitudinal transect in New Guinea, Diamond (1972: 27) found several pairs of species replacing each other abruptly, not always at the same altitudes; nor are all such pairs allospecies, though usually congeneric. The barbets *Pogoniulus pusillus* and *P. bilineatus*, not each other's nearest relative, occur sympatrically in some African habitats; in others there is an altitudinal replacement, and still elsewhere the bird of lower elevation extends to higher elevations in the absence of the second species (Short & Horne 1988). Sometimes an area is found between interbreeding allospecies where neither of them breeds, as in the titmice *Parus atricapillus* and *P. carolinensis* in some parts of their ranges (Brewer 1963).

When taxa doubtful as to subspecies or species are spatially disjunct the problem is more difficult. Vast numbers of populations are isolated in this way, on islands, in lakes, and on mountain tops. To each such case the taxonomist must bring all available data from study of congeneric or allied species and subspecies and the gaps between them; differences have to be sought in such possible isolating mechanisms as voice, behaviour, vagility, and others. Sometimes field or laboratory experiments are possible. Mayr (1969) provided a methodology for the evaluation of such taxa. Following analysis of information from all available sources, the taxonomist reaches a verdict as to the status of the disjunct populations. The verdict, to be sure, may be somewhat subjective or tentative, but an equally important result of the process is the enhancement of knowledge gained about the characteristics and biology of the organisms.

In summary, the taxonomist working with a relatively localized fauna or flora will usually encounter rather few problems as to species discrimination. When working with widespread groups, especially those with disjunct populations in varied habitats, it is the often the rule rather than the exception to encounter populations near the megasubspecies-allospecies boundary which require a judgmental verdict.

9, 10—MONOTYPIC SPECIES; POLYTYPIC SPECIES

These are are well known terms for designating species lacking recognized subspecies (monotypic) and species having recognized subspecies (polytypic).

11—MESOSPECIES*

This term is here proposed for polytypic species none of whose subspecies are deemed to be approaching species status. That is, it includes all those polytypic species, usually a large majority in any group of organisms, that are not megaspecies. Mesospecies, like megaspecies and superspecies, must be evaluated at one point in time, almost always the present.

12—MEGASPECIES

Crawford-Cabral (1986) proposed this term for species composed of megasubspecies. He employed the megaspecies in analyzing the evolution and zoogeography of a group of Rodentia as represented in the fauna of Angola, Africa.

Are all species that contain one megasubspecies comprised entirely of megaspecies? In a species such as the Northern Harrier *Circus cyaneus*, in which one megasubspecies occupies Eurasia and the other North America, that is obviously the case. But what of a species such as the Savannah Sparrow *Passerculus sandwichensis*, in which there is a megasubspecies *Passerculus* (*sandwichensis*) *princeps* on tiny Sable Island, off the coast of Nova Scotia, while elsewhere the species occupies most of North America, where it is separated into several lesser subspecies of the rank here named mesosubspecies? Almost surely, *princeps*, long regarded as a full species, is a recent post-glacial offshoot of the mainland population. Nevertheless, we conclude that the mainland population ranging from Alaska and Labrador to California should be called a megasubspecies, *P.* (*sandwichensis*) *sandwichensis*. If it and *princeps* were to attain species status, the step over the species threshold would probably not occur as a result of genetic changes in the mainland population, but rather in the small, isolated population of *princeps* itself, but this is not certain. For our purposes, this situation has been presented in oversimplified form, for there actually are 3 subspecies of *P. sandwichensis* along the coast of southern California and adjacent Mexico which, while not as strongly differentiated as *princeps*, nevertheless were at one time considered to be one or even 2 additional species. These 3 subspecies comprise a third megasubspecies, *P.* (*sandwichensis*) *rostratus*. Thus, the picture becomes more balanced, with a megasubspecies on or near each coast and the third occupying the intervening continent (Zink *et al.* 1991).

In our 1976 paper introducing the megasubspecies we did in fact conclude that conferring that status on one unit of a species automatically confers that status on the other population(s). Thus we wrote (1976: 163): "Although the term megasubspecies would often refer to a population occupying a small range, as on an island, this status confers like status on the remaining group or groups . . . of populations."

We have minimized our use of the term "sister" taxa, because it is a cladistic term that most cladists restrict to *only* 2 taxa. Yet we know that there frequently are more than 2 megasubspecies in a megaspecies, or allospecies in a superspecies. To be sure, it cannot be demonstrated that the allospecies in a superspecies, when more than 2, split simultaneously. For all practical purposes, however, one may assume that they did; such assumptions are as nothing compared with those often made when fossil taxa that diverged aeons ago are considered as sister groups. In any case the exact points of bifurcation are apt to be so close in time as to be essentially simultaneous.

A major fault of the cladistic approach, in our view, stems from the very fact that taxonomic status is determined strictly by the branching (furcation) points, and differentiation is ignored or discounted. Yet there are many cases (e.g. Haffer 1974 pointed out a number of them) in which 3, 4 or even 5 forms evolved from a common ancestor, with their evolutionary history predicated (in this case) upon vicariant separation, such as a developing system of rivers about the Amazon, or fragmentation of forest by drought. If the result is 5 approximately equally divergent entities, we would consider all 5 as coequal mesosubspecies, megasubspecies or allospecies depending upon their degree of differentiation and our judgment concerning their reproductive isolation. Were all 5 to have originated exactly simultaneously, their divergence from that point would make it extremely unlikely that their simultaneous origin could ever be deduced from their morphology. Even if geological data allowed one to construct a 'true' cladogram, this would not necessarily be useful (differences in time between branchings may only be several hundreds of years); indeed, the last 2 populations to branch, by chance alone, might now be more divergent than are the others that separated somewhat earlier. Hence cladistic analyses are liable to indicate incorrectly the bifurcation of the taxa. Thus it seems appropriate to treat the 5 as coequal taxa.

Short *et al.* (1983) described such a case among 5 megasubspecies of Australian sitellas (*Daphoenositta chrysoptera*), all of which come together and interbreed, forming a 5-way hybrid zone in central Queensland. The determination of time factors in this divergence, as in many cases, is very difficult; and the analysis of their divergence through study of morphology is complicated by the evolution of 'white-headedness' in the megasubspecies *leucocephala*, which has obliterated various features of colour pattern useful in the other 4. The 5 taxa appear behaviourally alike and they are vocally not distinguishable (Short & Horne, *pers. obs.*). Since all 5 hybridize *inter se* to the same extent, there appear to be no incipient isolating mechanisms in any one of them. Cracraft (1989) treats these sittellas very differently, using the phylogenetic species concept. He disregards the fact that the 5 are vocally similar if not identical, and the mesosubspecies that are also found among some of the 5 megasubspecies. Using primitive-derived character states that apparently are put forward *ad hoc* (some of his characters are affected, for example, by albinism in *leucocephala*, and for others there is simply no indication of which condition is 'derived'), he treats all 5 as 'species' and presents a cladogram of supposed relationships among the 5 for which we see no historical or morphological bases. In addition he ignores the extensive hybridization among the 5 diverse 'species'. The resulting products of interbreeding perforce become 'interspecific' hybrids. These occupy large areas and number tens if not hundreds of thousands of individuals. It is misleading to consider the 5 taxa as anything but coequal megasubspecies. Since the geological data often are unavailable or controversial in such cases, cladists may proceed by subjectively designating branching points based upon morphology and degree of divergence, thus producing a branching hierarchy (cladogram) which may be completely in error. As noted, the same considerations apply to allospecies.

13—ISOSPECIES*

We introduce this new term to designate a species that is not a member (allospecies) of an existing superspecies, that is, has no contemporary sister species. To be sure, many such species evolved as allospecies of a superspecies whose other members have become extinct, or, in some instances, may have evolved into new superspecies with their own contained allospecies. Chance events such as presence or absence of barriers, or differing rates of evolution, could bring about such a result. In other instances an isospecies may arise as a result of phyletic evolution.

14—ALLOSPECIES

Since an allospecies is one component of a superspecies, see also the discussion of that unit. Having concluded that both disjunct and parapatric taxa should be subsumed under allopatry, we disagree with Prigogine (1984, 1985), who limited the term allospecies to disjunct taxa and call those whose ranges are in contact 'paraspecies'.

Priogogine's 'paraspecies' is just one of many descriptive and potentially confusing labels that could be applied with reference only to the presence and amount of contact which obtains between allospecies. One could, for example, give 'allospecies' different names depending upon how far apart they are geographically, or 'paraspecies' likewise based on the extent of their contact, or differentiate between 'partly sympatric allospecies' as to the extent of their sympatry (small, moderate). Any or all of such distinctions would result in confusion. It matters greatly in analysis whether parapatric contact occurs along an interface 100 m, 100 km or 1000 km long, but such information should not be brought into definitions of taxa. Indeed the extent of parapatry and whether or not some sympatry occurs throughout a long, more or less abutting area of contact usually is incompletely known, and often is inferred from very few sites. Determination of parapatry requires one to verify that individuals of 2 allopatric populations can make contact in the breeding season. This requires that the observer is at the right place at the right time, particularly in cases of altitudinal parapatry, as non-breeders may wander out of the breeding range. We prefer to use 'allospecies' as above, whether the allospecies are disjunct, parapatric or (usually marginally) sympatric. Except that subspecies cannot be sympatric, we note that the same confusing terminology could be used for them—for example, various terms could be applied, such as 'parasubspecies' and 'allosubspecies'; such terms we think would be ill-advised. It seems better to restrict the number of terms and to have them refer to important levels of speciation intrinsic to the taxa, and thus not based upon chance extrinsic factors; then they will be of broader utility.

In parapatric allospecies, sporadic, marginal, or temporary overlap is probably the rule rather than the exception. Also, allospecies may be broadly sympatric in the off-season. Sometimes, as noted above, there may be a narrow zone between two allospecies in which neither occurs. More commonly, small, transient colonies of one or the other of a pair of allospecies exist within the boundaries of the other. In such situations, often in conjunction with a patchy environment, 2 allospecies (some would say former allospecies) are now sympatric over considerable areas, although the actual contacts, because of environmental preferences, may be hardly greater than in more conventionally parapatric species. The Eastern (*Sturnella magna*) and Western (*S. neglecta*) Meadowlarks studied by Lanyon (1957, 1962, 1966) are sibling species, have no close relatives, differ greatly in song and alarm notes, and overlap over a wide zone in central North America. There is occasional ineffective hybridization. The Indigo (*Passerina cyanea*) and Lazuli (*P. amoena*) Buntings provide a similar example (Sibley & Short 1959), with more hybridization and expanding overlap; eastern *cyanea* now appears in pockets far into the western North American range of *amoena*. Clearly these are or were allospecies, and their interactions and those of similar pairs provide excellent object-lessons for analyzing various aspects of speciation. Such forms, still able to interbreed and interacting ecologically with increased sympatry (ecological separation, interspecific territoriality) might be designated 'emergent allospecies'. This could be applied as well to cases of expansion of one allospecies into the range of another, with hybridization restricted to the advancing forward line of the invading allospecies, after which interbreeding is much reduced or ceases, the forms being in partial sympatry (e.g. the woodpeckers *Picoides syriacus/major* mentioned above and the titmice *Parus cyaneus/caeruleus* in Europe, discussed by Short 1969: 90–91; see Hewitt 1989).

Another remarkably complex case is afforded by 2 wood-warblers, *Vermivora pinus* and *V. chrysoptera*, which occur in patchy habitat over much of eastern North America (Gill 1987). They are sympatric in some areas and allopatric in others. Though the species' identities are not undermined, the 2 hybridize fairly freely, producing an array of hybrid phenotypes, 2 of which are so frequent and so distinct that they were described as species. *Vermivora pinus* is moving northwards, usually replacing *chrysoptera*, but with at least one pocket of the latter "left behind" in somewhat atypical habitat (Frech & Confer 1987). As a further complication occasional individuals learn the song of the 'wrong' species.

The behavioural interactions, general similarity, and occasional hybridization in such pairs demonstrate that they are allospecies. Careful analysis and weighing of evidence is necessary in determining their status and what they reveal about the dynamics of speciation and allied processes. Expanding allospecies with overlap but still some hybridization may be approaching the limit of allospecies, but with 'backward' shifts still possible, perhaps due to man's persistent modification of the environment.

The attention given to such taxa reflects their importance. One difficulty in considering partly sympatric pairs to be (still) allospecies is that in sympatry they may be mixed, and possibly confused with, species that are still interacting 'sexually' and ecologically in one way or another, but which are beyond the point where they can be properly called allospecies. Broadly overlapping congeneric species, perhaps formerly allospecies, may interact to some degree, and even species representing different genera can interact strongly, appearing like emergent (congeneric) allospecies. For example 2 wrens, *Thryomanes bewickii* and *Troglodytes* *aedon*, still hold interspecific territories, even though they are usually placed in different genera (Root 1969). Some might prefer to use Ripley's (1945: 338) term "interspecies" pair or group in such cases until their interactions have been well-studied and their relationships are clarified.

As noted earlier, the analysis of disjunct, closely allied taxa is difficult and sometimes subjective. Still, the gamut of possible shades of relationships is the same for disjunct, parapatric and partly sympatric sister taxa; what differs critically among them are the possibilities for interactions, and these determine the amounts and kinds of data they can provide, and the techniques that are available for studying them.

15—SIBLING SPECIES

Sibling species are ones that are difficult to distinguish phenotypically, such as the Eastern and Western Meadowlarks mentioned above. They will almost certainly belong to the same genus, but may not necessarily be the most closely related species within the genus, though that will often be the case. The classic example is of the fruit flies *Drosophila pseudoobscura* and *D. persimilis*, which can be separated phenotypically only by refined statistical analysis of measurements from large samples. Yet these 2 are completely cross-sterile and hence *ipso facto* species. Such sibling species are being unmasked commonly among insects; they exist but in far smaller numbers in vertebrates. The term is subjective and largely one of convenience and there is no 'test' or absolute criterion for sibling species. They may be either sympatric or allopatric, but the sympatric ones receive the most attention because they immediately pose problems as to how such at least superficially similar species can coexist. Allopatric sibling species are less apt to be detected unless it is found by chance that they are intersterile. In a few cases among birds, for example the many all-black crows and ravens of the widespread genus *Corvus*, there are numbers of both allopatric and sympatric sibling species.

Many sibling species evolve as an end result of divergence in isolation, and only later (sometimes) become sympatric; their antecedents, ranging from demes to megasubspecies, must be even more difficult to detect. The antecedent populations would not fulfill the requirement for formal subspecies since they would probably not be 'visibly different'. As a practical matter, it seems unwise to name such 'proto-sibling species' when they are suspected. There is a special challenge to the taxonomist to evaluate allopatric populations very carefully in groups well known to have sibling species, for example, among birds: *Corvus*; larks, Alaudidae; tyrant-flycatchers, Tyrannidae; and bulbuls, Pycnonotidae.

The 8 terms here advocated for various species-level taxa are not all mutually exclusive. A species may be monotypic or polytypic (but not both). A polytypic species may be either an isospecies or a mesospecies or a megaspecies. An isospecies cannot also be an allospecies, but an isospecies or an allospecies can also be a monotypic species, or a mesospecies, or a megaspecies. In theory, any of the others could be a sibling species.

16—GENUS

Higher classification is based upon the grouping of species in clusters of varying degrees of relationship, and is thus a scheme of hierarchies in the

Linnaean system of classification (genus, tribe, subfamily, etc.). These hierarchies are a result of evolution, with its speciation, adaptive radiations and extinctions. Thus higher classification is based on reality; but it also has a subjective element in that each cluster of species is, to a degree, unique. It is a matter of opinion as to how closely related a group of species must be to constitute a genus or a group of genera to constitute a family. Some species are so distantly related to any contemporary ones that they are best left in monotypic genera. For 'splitters' (taxonomists using many small genera) or 'lumpers' (those employing very broad genera) one can only counsel moderation. The genus has as its only function (aside from reducing the number of species names required), that of indicating groups of related species, but it must not be so inclusive as to impinge on the next higher category (tribe, subfamily, family). Nor can the number of categories be arbitrarily established; above we mentioned one, the tribe, not used by Linnaeus. The genus and subgenus, however, are 'official' categories, with established rules for their nomenclature.

The binomial system does have one serious flaw: changes in the genus' name affect both biologists and the general public. Yet new information as to a species' relationships may make nomenclatural changes mandatory; honest differences of opinion may do the same, e.g. one taxonomist being more impressed by certain morphological, behavioural or other peculiarities of a species, perhaps considering it as a monotypic genus, than is another who allows for more differences among congeneric species). Again, one can only recommend holding changes to a minimum; official check-lists, revised occasionally, help. More drastic solutions, such as using very broad genera and conducting the finer details at the subgenus level (Amadon 1966a) or using a mononomial system (Michener 1964) have met with little interest. Numerical systems may, to be sure, be used with computers (Little 1964), but names are needed also: it is easier to remember a hundred names, even Latin ones, than 4 or 5 numbers replacing a name.

One should attempt to keep the criteria for genera and other higher categories consistent across groups and time. This has heuristic value in that, e.g., a list of the species in an ecotype will contain genera that are roughly equivalent for plants and animals. Likewise fossil biotas, which often consist of a mixture of extinct and living species, can be meaningfully compared as a unit or with other biotas, and included with them in classifications.

Perhaps it is worth stressing the obligation of the systematist to place his studies in perspective by considering the next higher and next lower category to that with which he is dealing. That is, species of a genus ought not to be studied or revised without considering the taxonomy of related genera, and the final results ought to take them into account. A genus (or species, or family) should not be studied, as it were, in a vacuum. Likewise, although political or economic factors sometimes force a narrow focus upon a taxonomic investigation, studies that are geographically restricted (to a state, country or region), although the taxa involved are widespread outside that restricted area, should sometimes be postponed. Caution is especially advised when working with a taxon at the fringe of its range, or taxa which are at the periphery of the range of the group to which they belong. If avoidable, a speciose tropical genus should not be revised if one can study in detail only a handful of its species which marginally penetrate an adjacent temperate region.

17—SUBGENUS

The subgenus is a formal category and if one recognizes subgenera in a genus then all of its species should be assigned to one subgenus or another, according to their affinities. A systematist revising a genus containing some little known or problematic species may prefer to avoid this formal category and use the informal species group; then species presenting such problems may, so to speak, be left 'dangling' without the necessity of assigning them formally. It is better to employ subgenera than to oversplit genera. In groups in which many genera were named that now seem superfluous, such names are often available for subgenera. It is unwise to use subgenera in some genera of a family but not in other equally diverse ones, though if some are much better known than others this may ensue. A few taxonomists go to the extreme of decrying generic 'splitting', meanwhile flooding the literature with subgenera.

18—POLYTYPIC GENUS

As defined—a genus containing more than one species.

19—MONOTYPIC GENUS

The genus is defined as a group of species; hence a genus with but one species seems like a contradiction in terms. Nonetheless, some species, indeed considerable numbers in certain groups, are so distinct and lacking in close relatives that they must be admitted as monotypic genera. If we had a complete fossil record some of them would be found to have contained other species now extinct. Indeed many monotypic genera are relicts, but some of them may have contained but one species for a very long time, e.g. *Gingko, Latimeria* and *Sphenodon*. Still others are probably the end products of phyletic evolution and never contained other species. Among birds, *Balaeniceps* or *Rhynochetos* might be candidates. Finally, during adaptive radiations, species may evolve with relative rapidity, thereby producing monotypic genera that may or may not later bud off additional species. Thus, at any point in time some species have very close relatives, others only very remote ones, while the majority fall between.

20—QUASI-MONOTYPIC GENUS

This term was coined by Amadon (1968) but the concept has been employed by others (e.g. Diamond 1972: 305). Many genera consist of a single superspecies and are, for some biogeographical purposes, equivalent to a single species. Thus the skimmers, *Rynchops*, a superspecies with 3 species, 1 in Africa, 1 in India, and 1 in the Americas, are so similar and specialized that it is unlikely that sympatry will ever ensue; this genus is quasi-monotypic.

21—SPECIES GROUP

The species group might be regarded as an informal, un-named subgenus. Because it is informal, not all the species in a genus have to be assigned to a species group and indeed the information is often lacking to do so. With further data, species groups in a genus may be replaced by formal subgenera, or this may be deemed unnecessary. Obviously, use of the species group does not burden the memory with more names (usually a species group is referred to by the specific name of one of its best known or widespread species). The purpose of both categories, of course, is to aid in understanding relationships and lines of evolution, especially in species-rich genera (see Mayr & Short 1970: 102–103).

Paramount is the point that the species in a group are more closely related, often considerably more closely related, to one another than is any of them to any other species in the genus outside the group. It is implicit that there are gaps between species groups. In very large genera, it sometimes may be desirable to set up species groups within subgenera.

Haffer (1986a) has more rigorously, and we feel unnecessarily, redefined species groups to equate them with putative former superspecies whose component species are actually or potentially sympatric. This would severely limit the use of species groups because allopatric species (that were formerly all allospecies of a superspecies) can evolve further in isolation to the point at which their relationships are those of a species group (or, with one or more other sympatric or allopatric species, they may form a species group). Also a superspecies, or several superspecies, may form a species group together, or along with, one or more isospecies. Extinctions of species or allospecies may leave isospecies that are taxonomically somewhat isolated in their genus, though their relationships with other isospecies and superspecies may be sufficiently close to include them in a species group.

The barbet genus *Trachyphonus* contains 5 species interrelated as follows: (a) a species group *erythrocephalus-margaritatus-darnaudii*, of which the first 2 make a superspecies, while *darnaudii* is a megaspecies; (b) another megaspecies *purpuratus*; and finally (c) a mesospecies, *vaillantii* (Short & Horne 1985a,b, 1988). This illustrates the use of a species group in a way that would not be possible under Haffer's (1986a,b) proposal, by which we feel much is lost in encumbering and narrowing the use of 'species group'.

22—SUPERSPECIES (see also discussion of allospecies)

The allospecies of a superspecies are more closely allied to one another than to any other species. Some genera, subgenera or species groups consist of a single superspecies, but many contain species not so intimately related. Allospecies are often the equivalent of the cladist's 'sister species' (or for some, e.g. Cracraft 1989, 'sister megasubspecies').

In formal taxonomic treatments the use of brackets to indicate superspecies is recommended (Amadon 1966b). In other contexts this may be accomplished by using footnotes (A.O.U. 1983), by the use of braces (Short 1982), by connecting allospecies with hyphens (Diamond 1972: 321), or by the use of superscripts (Amadon & Bull 1988).

In listing allospecies of a superspecies, the first named allospecies does not always appear first, because of relationships, primitive-derived sequences, or geographical conventions. In some local or regional publications, not all of the allospecies in a superspecies may be listed. Still, it is often useful to know that a species has allospecies elsewhere. For example in a list of the bird species of Africa *Haliaeetus* [*vocifer*] indicates that *vocifer* has one or more closely related species (allospecies) elsewhere (in this case a species in Madagascar).

The designation of superspecies is often tentative. The Indian and African elephants do not form a superspecies, but without a fossil record that might not be so obvious. Question marks may be used to indicate doubt, or one may say "species 'X' and species 'Y' *may* constitute a superspecies". Such qualifications do not detract from the utility of the concept (Amadon 1966b, Mayr & Short 1970).

Haffer (1986b) has rigorously subdivided superspecies into 'First Order' superspecies (those we have discussed above); and 'Second Order' superspecies (or 'megasuperspecies'). The second order superspecies contain either 2 (or presumably more) of his first order superspecies, or a mixture of one (or more) first order superspecies with one (or more) species not part of a first order superspecies, i.e. with what we term isospecies. While every attempt to clarify and denote relationships is to be applauded, there is greater subjectivity in Haffer's approach; for example, one must guess about extinctions of former allospecies. We suppose one could go further, to 'Third Order' superspecies, and so on, but this would seem to compound the subjectivity at several levels, perhaps exponentially, with greater difficulty in distinguishing second order and third order superspecies, and even more potential for errors. We realize that many isospecies evolved as allospecies of superspecies whose sister allospecies became extinct. Proving this would indeed be difficult, as in the case of Haffer's (1986b, Fig. 1c) example of a second order superspecies formed from 2 first order superspecies, each of which apparently had suffered the extinction of one allospecies. By overly striving to be precise, Haffer has unduly restricted a more broadly useful terminology, coupled with the addition of greater subjectivity, and we think his categorizing of superspecies is not practical for general use. To be sure, specialists intensively studying a limited cluster of taxa may find it worthwhile to group them in various ways.

There has been an unfortunate tendency, evident, e.g. in Hall & Moreau (1970) and Snow (1978) to place all well-marked, congeneric, allopatric taxa into superspecies. This 'overinflation' of the superspecies, effectively to the level of the species group, has been criticized by Vande weghe (1988: 2550), indicating the crucial need to use all available information in making taxonomic decisions involving allopatric taxa. It is the task of the taxonomist to evaluate carefully all related allopatric taxa to determine whether they are monophyletic, and whether relationships are at the level of megasubspecies, superspecies, or species group. Faulty assignment of level (equivalent to 'upgrading' or 'downgrading') is wrong, no matter what the level, whether done intentionally (persons concerned about the conservation status of taxa may do this), or unintentionally (through failure to analyse appropriately the available data). Allopatry alone does not place a taxon in any one of these categories.

23—BIOGEOGRAPHICAL UNIT (or SPECIES)

This is the concept that is usually called a 'zoogeographical species'—one in which isospecies and superspecies are equated as biogeographic entities. That is, individual allospecies are not tallied separately. Since the concept applies equally well to plants, in which they would be called 'phytogeographic units', we suggest that biogeographic be used to cover both. Further, 'species' is somewhat misleading in this context, because superspecies, of course, are groups of species, not single species. We therefore believe the word 'unit' to be preferable.

As an example, assume that a chain of islands was colonized by 2 species of a family, the 2 not closely related (i.e. they represent different genera). Assume further that one of them is now a superspecies with 5 allospecies, each on its own island, while the second is still monotypic. If all the allospecies are tallied, it conceals the important fact that the family in question has colonized these islands only twice. Biogeographic units thus are useful in comparative studies of the diversity of different regions, and continents, as well as diversity of different groups within and between regions (see Mayr & Short 1970: 5).

In his check-list of the Pipridae and of the Cotingidae and elsewhere Snow (1979, see footnotes) equated 'zoogeographical species' with 'superspecies', citing Mayr & Short (1970). The latter, however, as we do here, treated zoogeographical species (or 'units') as including not only superspecies, but also non-allospecific species (isospecies). We feel that our usage and the distinction between zoogeographical units and superspecies have considerable heuristic value.

24—ASEXUAL POPULATIONS

The interchange of genes (e.g. 'conjugation' in *Paramecium*) apparently arose fairly early in the history of life and in higher organisms became sexual reproduction. The latter conferred such immense advantages by increasing heritable variability and hence adaptability that it has been dominant ever since (Vrijenhoek 1990). Nevertheless, some monocellular organisms (some bacteria) and a few advanced forms of life reproduce exclusively by asexual means. Most of them are plants and result from polyploidy; vegetative reproduction is much easier in plants and permits such sterile individuals to survive. Parthenogenic populations among animals are rarer, except for 'castes' in some social insects, but these are irrelevant here. Polyploids or sterile hybrids between species of animals have little chance of survival, but a few parthenogenic populations of lizards and other groups have managed to do so. Such instantaneously produced species, whether plant or animal, usually survive, when they do so, in raw, disturbed habitats (whether naturally so, or by humans), where competition is less.

Many species of plants, known by chromosome counts to have arisen by polyploidy, later again reproduce sexually. Occasionally fertile individuals do occur, and so great is the premium on genetic exchange that gametic reproduction has become re-established.

Are asexually reproducing populations or clones to be called species? Our preference would be to use some such term as 'pseudo-species' or 'quasi-species'. Nevertheless, so much literature, especially botanical, uses 'polyploid species' that we see little hope of a change. Hence one accepts a second major category of species to be called 'Asexual' or perhaps better 'Agametic' species. Other species are then Sexual or Gametic Species. The latter are so much more important and successful (except perhaps in some bacteria, viruses and the like) that the term species, without qualification, may be taken to refer to those in which an exchange of gametes occurs. If confusion arises, a simple alternative would be to agree that 'species' in quotation marks always refers to asexual populations.

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